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The Effects of Tree Crushing on Small Mammal Populations in South Central Alaska

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Renewable Natural Resources

by

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ABSTRACT

Vegetation surveys, snap trapping, and food habits analysis were conducted to reveal some of the relationships between small mammals and habitat disturbance by tree crushing in an Alaskan boreal forest. Tree crushing generally decreased red-backed vole (*Clethrionomys rutilus*) densities, increased meadow vole (*Microtus pennsylvanicus*) densities, and had little effect on shrew populations. Red-backed voles and masked shrews (*Sorex cinereus*) remained the dominant species before and after crushing. Crushing in mature hardwood forest types increased small mammal density and diversity. Crushing in black spruce and birch-spruce types reduced small mammal densities and increased species diversity.

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INTRODUCTION

Small mammals are thought to be one of the most important elements in cold dominated ecosystems. They greatly influence three major components of these ecosystems: the soil, vegetation, and predators which depend on them as food (Elton 1942, Pitelka et al. 1955, Thompson 1955, Pitelka 1957, Batzli 1971, 1975). Although the effects of small mammals on vegetation have been studied extensively, expecially in regards to forest regeneration, (Frank 1957, McKeever 1961, Ahlgren 1966, Gashwiler 1969, Sims and Buckners 1973, Pank 1974, Golley et al. 1975, Martell and Radvanyi 1977) little is known about the effect of vegetational changes on small mammal populations. This is particularly true of the arctic or boreal forest ecosystems found in Alaska.

The two major objectives of this study were: 1. Document the effects of the moose habitat manipulation program being carried out on the Kenai Peninsula on small mammal populations. 2. Determine if the food habits of small mammals might have an effect on the type of vegetation coming back in treated areas. This kind of information could allow more effective management of all species on the refuge.

The history of the Kenai National Moose Range is a story of fire and plant succession. Before the 1880's, the Kenai Peninsula lowlands were covered by mature spruce forests. That changed during the next 20 years when the forests were repeatedly burned by wildfires. Caribou were common before

the wildfires, but moose were reportedly scarce (Lutz 1960). Fire had set back plant succession and a large portion of the area had become a vast shrubland. The moose population quickly expanded in response to the abundant browse provided by these early successional stages and soon the Kenai Peninsula was famous for its large moose herds (Lutz 1960). As the shrublands were replaced by forest, the moose population declined. This pattern has apparently been repeated for as long as there have been wildfires (Sarber 1944, Spencer and Hakala 1964).

Although the Kenai National Moose Range was established in 1941 to protect and preserve the Kenai moose and its habitat, it is becoming increasingly difficult to do so. Oil development, refineries, and the increasing number of people living on the peninsula have made wildfires dangerous and feared. There is full support for the modern firefighting techniques that have tended to make wildfires on the peninsula a thing of the past.

In order to manage moose, wildlife managers on the Kenai National Moose Range were put in a difficult position. How do they protect and preserve the Kenai moose and its habitat while at the same time protecting the lives and property of the people living on the peninsula? Obviously some disturbance other than wildfires would have to be used to create the early successional stages that moose thrive on.

Several management options to regulate plant succession were controlled burns, herbicides, logging, or some type of mechanical habitat manipulation. Controlled burning was an obvious choice but met with little success (Spencer and Hakala 1964). Fuel moisture was often too high for burning or too low and the danger of wildfire too great. Herbicides were tried in the 1960's, but were costly and not very effective (US Dept. of Interior 1961, Spencer and Hakala 1964). Logging would have been a viable option except that the economics of Alaska does not make Moose Range timber marketable at this time (Johnson, per. comm.[1], Spencer and Hakala 1964). Mechanical disturbance of the vegetation was another alternative. At first, crushing with fleco drum rollers pulled by caterpillars was attempted. This technique created more browse for moose, but was expensive and slow (Spencer and Hakala 1964). In 1969, three 40-ton Letourneau tree crushers were purchased to crush various habitat types and create a more favorable habitat for moose. Over 6,000 hectares in five different locations have been crushed to date.

Although tree crushing is a technique for the management of a single species, moose, it affects every animal living in treated areas. The effect of the crushing program on other species is unknown. Small mammals are particularly susceptible to any habitat disturbance because

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[1]Personal communication from Mr. Al Johnson, forester, Kenai National Moose Range, Kenai, Alaska. Sept. 1978.

of their limited home range. Small mammals play a critical role in a complex food chain. They are not only important herbivores, but a major food source for many other species (Golley et al. 1975). Studying the impact of tree crushing on small mammals is an important first step in understanding the complex plant-animal interdependencies which are changed by habitat management programs.

STUDY SITES

This project was conducted on the 688,000 ha Kenai National Moose Range in south-central Alaska. The moose range is approximately 100 km south of Anchorage and encompasses most of the lowland boreal forest on the Kenai Peninsula. This area has been repeatedly burned since the 1880's (Lutz 1960). The resulting vegetation types form a mosaic pattern of uneven aged stands of regrowth and mature timber. The last two large fires on the peninsula occurred in 1947 (125,450 ha), and 1969 (35,200 ha). Areas used in this study were affected by those fires.

Cold dominated ecosystems are typically low in species diversity. The Kenai Peninsula is no exception. Plant species in mature and regrowth vegetation types are very similar. White spruce (Picea glauca), black spruce (Picea mariana), paper birch (Betula papyrifera), and quaking aspen (Populus tremuloides) are the dominant overstory species in both. The ground vegetation is usually a mixture of lowbush cranberry (Vaccinium vitus-idaea), moss (Sphagnum spp.), and lichens (Peltigera spp. and Cladonia spp.). Common species found throughout the various habitat types include willow (Salix spp.), fireweed (Epilobium angustifolium), bunchberry (Cornus canadensis), grass, primarily (Calamagrostis canadensis), and various types of mushrooms. The density of each species varies from site to site depending on the age of the stand, topography, and elevation.

Four study areas that have been treated by Letourneau tree crushers were selected for study (Fig. 1). The Marathon Road, Willow Lake, Moose Research Center, and Mystery Creek areas were all crushed as part of a moose habitat manipulation program being carried out by the US Fish and Wildlife Service. Tracts of mature timber as well as burned regrowth stands are scattered throughout these areas.

Trapping sites were selected after examining vegetation survey data in treated areas (Oldemeyer 1978). The vegetational description of each area and the sites within them is based on this information. Two sites were selected at the Marathon Road area. Six sites were selected at the Willow Lake, Moose Research Center, and Mystery Creek areas. In each study area, every site represented a different habitat type or location.

Marathon Road

A large fire in 1969 burned 35,200 ha near Kenai and it was in this area that the tree crushers were first used. Approximately 3,240 ha were crushed here during 1971 and 1972. Only burned areas were crushed. A site that was burned and crushed and an undisturbed site 7 km N.E. of Kenai along Marathon Road were sampled for small mammals. These sites were used to test traps, trapping patterns, bait preference, and to collect specimens for study rather than to obtain relative density estimates as was done for sites in the other three areas.

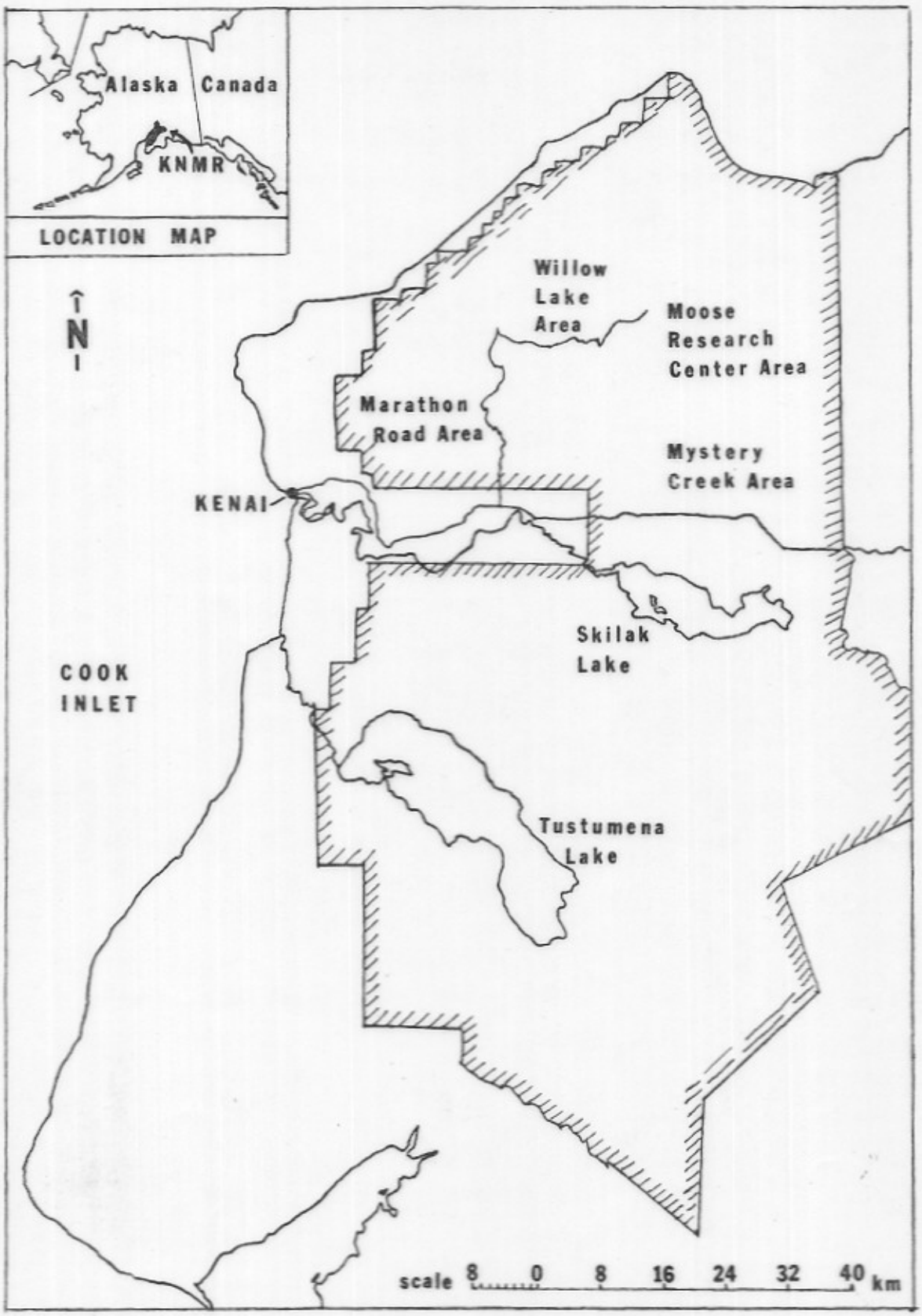

FIG. 1. Treated areas selected for small mammal study on the Kenai National Moose Range in south central Alaska.

The two sites along Marathon Road clearly reflect the results of disturbance in boreal forest types. The burned, crushed site has a high percentage of grasses and willow. There are patches of almost pure grass and abundant ground litter throughout the site. Mosses are abundant, but lichens and lowbush cranberry are rare. The mature site is similar to mature sites at Willow Lake and the Moose Research Center. It is a birch forest with scattered aspen and white spruce. There are few understory species other than mosses, lichens, and lowbush cranberry.

Willow Lake and Moose Research Center

The primary study area was located around Willow Lake where 460 ha were crushed during the winter of 1974-75. Willow Lake is approximately 40 km N.E. of Kenai and 7 km N.W. of the Moose Research Center. A large fire burned through this area in 1947. Many scattered habitat types, rolling hills, and numerous lakes typify the Kenai lowlands.

The Moose Research Center located near Willow Lake was also sampled for small mammals. Approximately 525 ha were crushed in and around the moose pens during the fall and winter of 1975-76. Like the Willow Lake area, vegetation in the Moose Research Center was affected by the 1947 fire. Habitat types in these areas are very similar although terrain at the Moose Research Center tends to be flatter. Both of these areas were sampled for the relative density of small mammals in crushed and uncrushed habitat types.

Three habitat types were selected for study in these two areas. Each type was represented by a crushed and uncrushed stand. Mature birch-white spruce, birch-black spruce regrowth, and black spruce regrowth were the three types sampled for small mammals. These habitat types occur throughout the peninsula and compose a large portion of the vegetation in the study areas.

Mature uncrushed sites: The mature uncrushed sites have very little understory vegetation and are predominantly mature birch forests with scattered aspen and white spruce. These sites were not burned by the 1947 fire and the trees are now 10-20 m high and 15-35 cm in diameter. There are occasional patches of Spirea sp. and devils club (Echinopanax horridum), however, shrub-type vegetation is scarce. Lowbush cranberry, mosses, and lichens are the dominant understory vegetation.

Mature crushed sites: The mature crushed sites are characterized by a large amount of standing debris and aspen regrowth. The tree crushers easily push over the larger trees but can't chop them into the 1 m sections as they do smaller regrowth vegetation. As a result, mature crushed sites are a tangled series of mature trees lying up to 2 m above ground level. The mature crushed sites produce the largest amount of aerial debris of any site. For unknown reasons, the Willow Lake area responded much better to crushing than the Moose Research Center area (Tables 1,2). The

TABLE 1. Vegetation analysis for the Willow Lake area.

Vegetation	Black Spruce		Birch-Spruce		Mature	
	Crushed	Uncrushed	Crushed	Uncrushed	Crushed	Uncrushed
Tree°	0	0.4	0	0	0	8.4
Shrub+	4.5	7.7	20.5	27.4	7.7	0.9
Herb*	25.3	6.8	4.4	4.7	22.7	4.1
Grass*	6.9	0.4	0	0	2.4	0
Woody*	4.2	2.2	9.6	2.2	18.1	1.6
L. Cranberry*	13.4	12.5	4.3	7.6	3.3	2.8
Lichen*	1.4	16.5	5.5	13.2	0	0.4
Moss*	5.8	11.1	3.3	3.5	3.2	4.1
Ground Debris*	16.8	1.8	7.2	5.8	4.3	0.8
Aerial Debris*	0.5	4.2	2.3	10.0	11.8	3.6

° Average number of trees per plot BAF 10% (basal area factor).
+ Average number of shrubs over 40 cm high per $5m^2$ plot.
* Average percent ground cover under 40 cm high per $0.1m^2$ plot.

TABLE 2. Vegetation analysis for the Moose Research Center.

Vegetation	Black Spruce		Birch-Spruce		Mature	
	Crushed	Uncrushed	Crushed	Uncrushed	Crushed	Uncrushed
Tree°	0	0.4			0	8.1
Shrub+	0.9	6.4		12.1	11.8	2.5
Herb*	3.0	4.7			11.6	16.4
Grass*	1.0	1.1			0.3	0
Woody*	0.2	0.5			5.3	3.4
L. Cranberry*	5.9	8.4			2.7	9.0
Lichen*	7.2	7.8			0	9.6
Moss*	4.0	13.6			7.0	14.3
Ground Debris*	2.7	1.2			10.5	26.5

° Average number of trees per plot. BAF 10% (basal area factor).
+ Average number of shrubs over 40 cm high per $5m^2$ plot.
* Average percent ground cover under 40 cm high per $0.1m^2$ plot.

different response is evident when comparing the total cover by plants in the $0.1m^2$ plots in each site. The mature crushed site at Willow Lake had 49.7% aerial cover compared to 26.9% cover for the Moose Research Center.

Birch-Spruce uncrushed sites: The 1947 fire destroyed much of the vegetation in these areas and some of it grew back as a mixture of birch and black spruce. The birch-spruce regrowth sites are dense regrowths of black spruce and paper birch with a lowbush cranberry, lichen, and moss understory. The regrowth vegetation is up to 7 m high and creates the densest shrub cover of any site. Willow Lake averages 27.4 shrubs per $5m^2$ plot (Table 1) while the Moose Research Center averages 12.1 (Table 2). The comparatively lower shrub cover of the Moose Research Center still represents a 50% higher shrub cover than any other uncrushed site. The birch-spruce uncrushed sites also have the highest amount of standing debris of any uncrushed sites. Burned, dead spruce litter the sites and provide almost as much cover as downed timber in the mature crushed sites.

Birch-spruce crushed sites: Crushing the birch-spruce regrowth changed the aerial debris to ground debris and stimulated browse regrowth. Lowbush cranberry, mosses, and lichens were exposed and have survived only under debris or regrowth vegetation. Although crushing reduced their densities, no other species replaced them as the dominant understory vegetation. The birch-spruce crushed sites appear to

be groupings of ground debris, birch regrowth, and occasional spruce seedlings.

Black spruce uncrushed sites: In these sites, black spruce came back in almost pure stands after the 1947 burn. Black spruce uncrushed sites are composed of black spruce, lichen, lowbush cranberry, and moss. Dead, burned black spruce are scattered throughout the sites indicating that before the fire, the sites weren't very different than they are now. The black spruce uncrushed site at Willow Lake (Table 1) is the most diverse site in terms of understory variation. Ridge tops may be almost bare while low, wet areas may be sedge covered. The black spruce uncrushed site at the Moose Research Center (Table 2) is in a flat area and understory vegetation varies less within that site. Black spruce in these sites average 4-8 m in height.

Black spruce crushed sites: Crushing black spruce causes a dramatic decrease in the amount of aerial cover from living and dead material. The black spruce crushed site at Willow Lake was very slow to respond and for the first three years remained almost barren. Above average rainfall during June and July may have caused the tremendous regrowth in annual plants and grasses during 1978. Nearly all of the cover in that site is under 40 cm high. The black spruce crushed site at the Moose Research Center hasn't responded well to crushing as yet (Table 2).

Mystery Creek

The eastern edge of the 1947 burn near Mystery Creek produced a large area of black spruce regrowth. Over-browsing of hardwoods by moose gave spruce a competitive edge and the result was a large tract of black spruce 4-8 m high with a lowbush cranberry, moss, and lichen understory. Browse species are still present in the area but many are severely damaged by heavy browsing.

The Mystery Creek area was first crushed during the summer of 1963 when 16 ha were treated by D-8 caterpillars pulling fleco-rollers. Reportedly, browse in this area responded favorably (Johnson, per. comm.[1]) but moose concentrated in the site and severely over-browsed it.

The area was crushed again in 1977 and 1978 by Letourneau tree crushers. Summer as well as winter crushing was conducted to determine the most effective means to stimulate browse regrowth. All of the crushing was done in black spruce regrowth stands. Sites in this area were sampled to reflect the effect of crushing over time as well as at different seasons of the year.

Black spruce, summer 1963 crushed site: The 1963 crushed site is a black spruce regrowth with lowbush cranberry, moss, and lichen understory. The trees are 2-4 m high and scattered. Crushing knocked standing dead timber to the ground. Stunted

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[1]Personal communication from Mr. Al Johnson, forester, Kenai National Moose Range, Kenai, Alaska. Sept. 1978.

browse species remained scattered throughout the site. Crushing increased ground debris and reduced spruce densities. This site was crushed during the summer and there are still locations where the mineral soil was exposed and remains barren.

Black spruce uncrushed 'A' site: An adjacent uncrushed stand of 1947 burn black spruce was used for comparison with the black spruce, summer 1963 crushed site (Table 3). The black spruce uncrushed 'A' site contains 4-8 m high spruce and many dead burned poles. The understory is composed of lowbush cranberry, lichens, and mosses. It is similar to black spruce uncrushed sites at Willow Lake and the Moose Research Center.

Black spruce, winter 1977 crushed site: One kilometer south of the black spruce, summer 1963 crushed site, 65 ha were crushed during the winter of 1976-77. Vegetation in the winter 1977 site has started to respond and several species of browse are appearing (Table 3). Most of the shrubs are under 40 cm high and scattered. The dominant understory species are still lowbush cranberry, mosses, and lichens. Grasses are on the increase.

Black spruce, summer 1977 crushed site: Sixty-five hectares were crushed during the summer of 1977 in an attempt to disturb the soil and provide a seed bed for aspen, willow, and birch. Crushing in the summer disturbed the soil in conjunction with eliminating most of the standing black spruce.

TABLE 3. Vegetation analysis for the Mystery Creek area.

Vegetation	Black Spruce			
	Summer		Winter	
	Crushed 1963	Uncrushed 'A'	Crushed 1977	Uncrushed 'B'
Tree°	0	0	0	0
Shrub+	11.1	7.1	4.4	6.2
Herb*	7.6	6.3	4.8	7.3
Grass*	2.2	2.3	1.2	2.3
Woody*	1.2	1.7	5.1	0.8
L. Cranberry*	12.1	20.0	18.6	11.6
Lichen*	8.3	14.8	8.3	14.5
Moss*	4.9	6.6	3.7	15.6
Ground Debris*	4.3	1.4	3.7	0.7

° Average number of trees per plot BAF 10% (basal area factor).
+ Average number of shrubs over 40 cm high per $5m^2$ plot.
* Average percent ground cover under 40 cm high per $0.1m^2$ plot.

Blades on the crushers wheels cut and lifted out portions of the vegetation to expose mineral soil. In 1978, the site hadn't yet responded to the crushing, other than by the growth of some fireweed and a few birch shoots.

Black spruce, winter 1978 crushed site: Another 65 ha tract crushed during the winter of 1978 looks very much like the black spruce, summer 1977 crushed site except the soil layer was not disturbed. Both of these sites are littered with newly downed spruce and old burned poles. Ground vegetation is still dominated by lowbush cranberry, lichens, and mosses. Patches of lowbush cranberry were drying out in both sites and, without the tree cover, that trend may continue.

Black spruce uncrushed 'B' site: A control site was selected between the black spruce, summer 1977 crushed and black spruce, winter 1978 crushed sites. The black spruce uncrushed 'B' site is a black spruce regrowth stand with a lowbush cranberry, moss, and lichen understory. Trees are all about 4-8 m high and not particularly dense. Dead, down and standing timber is scattered throughout the trees. It is very similar to the black spruce uncrushed 'A' site.

METHODS

Vegetation Methods

The methods used to analyze the vegetation at each site were those used by personnel of the Denver Wildlife Research Center studying vegetation on the Kenai Peninsula (Oldemeyer 1978). Vegetation in each site was sampled by using point-sampling (Bitterlich 1947, cited by Kulow 1965) to estimate the basal area of mature trees, 1X5 m quadrats to obtain shrub densities and 2X5 dm quadrats to sample the aerial cover of all plants under 40 cm tall. The Willow Lake area was also sampled by a 5 m transect for an estimate of aerial debris. Twenty-five randomly selected locations were sampled within each study site.

Trapping Methods

Small mammal populations were sampled by trapping with museum special snap traps during the summer months of 1977 and 1978. In 1978, the traps were slightly modified to increase their effectiveness at catching shrews (Appendix A). In 1977, the only area trapped was Willow Lake. Four trapping periods were conducted that year, one in July, two in August, and one in September. In 1978, trapping was conducted in all areas. The Willow Lake area was trapped in three periods, one each during May, August, and September. Both the Moose Research Center and Mystery Creek areas were trapped once in May and once in September.

Two parallel rows of 12 transects, 75 m long and 30 m apart, were layed out in each site (Fig. 2). Four of these transects were randomly selected with no repeats for trapping during each trapping period. Fifteen museum special snap traps baited with peanut butter, oats, and bacon grease (Davis 1956, Beer 1964) were set 5 m apart along each selected transect. Whenever possible, the traps were set under debris or vegetation to protect them from birds and rain. Traps were checked daily for four days and rebaited when necessary. At the end of a trapping period, each site had 240 trap nights for a total of 1440 trap nights per area. All sites within an area were trapped at the same time. Trapping patterns were the same for all sites and areas during each trapping period. The relative density of the various sites was determined by a direct comparison of numbers of captures per site and area.

Red-backed voles and masked shrews were the only species abundant enough to compare statistically. Other species were either restricted to one site or at very low numbers. One-way analysis of variance tests were used to compare the effects of site and time on trapping success. Data gathered from each site were compared by using Duncan's new multiple-range test (Steel and Torrie 1960). Chi-square was used to test for significant differences in the sex ratios between sites and areas. The Shannon-Wiener Information Measure (Wilson and Bossert 1971) was used to compare species diversity of sites and areas sampled. The information from each

Examples shown:

O - Lines selected for trapping May 1978.

X - Lines selected for trapping Sept. 1978.

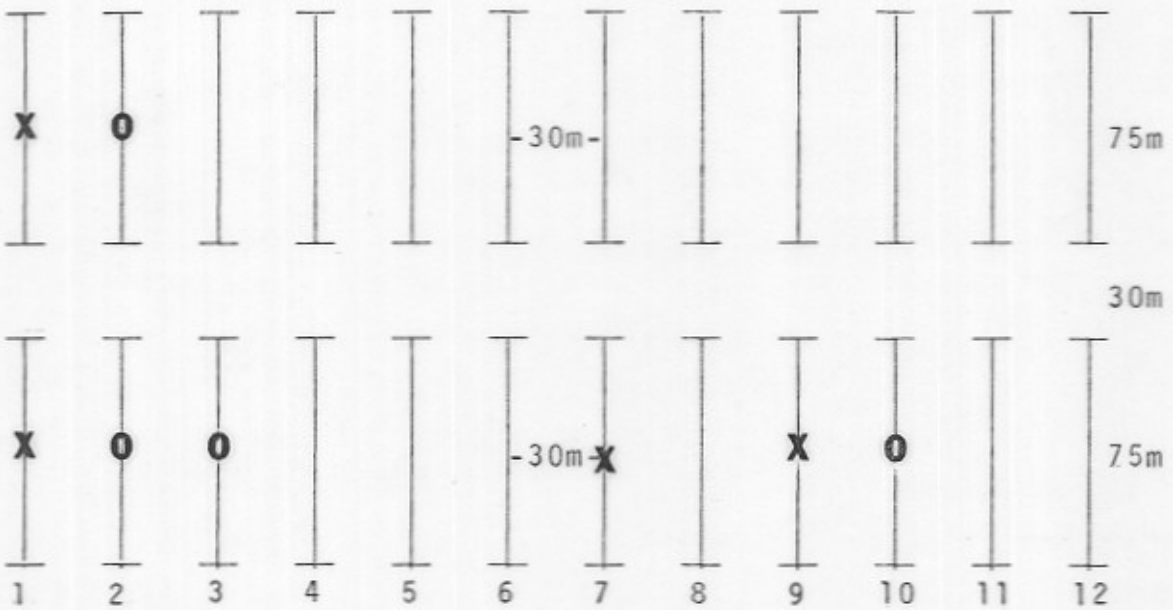

FIG. 2. Examples of random trapping patterns used in each site during a trapping period.

study site would show if the densities of the small mammal populations varied with habitat type, treatment, or time.

The number of mammals and birds caught as well as the number of snapped but empty traps was recorded. Captured mammals were stored in double plastic bags (Banks 1965) and frozen for later examination. All mammals caught were weighed, examined for age, sex, reproductive condition, and parasites (Davis 1956, Hall and Kelson 1959, Woolfenden 1959, Hall 1962, Pucek and Lowe 1975). This would indicate any structural differences in the various populations as well as in their densities. Mammals were identified by skull and pelt characteristics (Hall and Kelson 1959).

Food Habits Methods

Small mammals have been shown to affect the revegetation of disturbed sites by consuming the seeds and seedlings of various plant species (Pank 1974). The stomach contents of voles caught in the Willow Lake study area during the summer of 1977 and spring of 1978 were examined with the aid of dissecting and compound microscopes to discover if voles on the Kenai Peninsula could be affecting the revegetation of crushed areas. The dissecting scope was used to identify parasites (Appendix C) and insect remains. Permanent slides of stomach contents were made following the standard procedures recommended for microscopic stomach analysis (Baumgartner and Martin 1939, Dusi 1949, Williams 1962, Dearden

et al. 1972, Wolff 1978). Analysis of the slides was done by comparing plant materials found in the stomachs with reference material collected from living plants. Examination of stomach contents and reference slides was done under a compound microscope set on 100X. Several weeks were spent examining reference and stomach slides for familiarization with cell structures and plant identification (Dusi 1949). Twenty observations were made per slide, each slide representing one stomach. The location of each observation was random with no repeats. A field of view with no plant fragments was not counted, but the stage was moved until plant material was present (Williams 1962). If material was present, but could not be identified, it was recorded as an unidentifiable observation. Almost every field of view contained some unidentifiable material. The presence of every identifiable species of plant was recorded per field of view. A single field of view could contain several different species. It was assumed that relative occurrence of a food species on a slide was directly proportional to relative volumes consumed (Sparks and Malecheck 1968).

RESULTS

Species Diversity of Small Mammals

In 15,840 trap nights of effort during 1977 and 1978 over 1400 small mammals were captured. Only six species were represented. Red-backed voles and masked shrews were the most common. Meadow voles, vagrant shrews (Sorex vagrans), pygmy shrews (Microsorex hoyi) and northern bog lemmings (Synaptomys borealis) were rare. In the total catch, red-backed voles comprised 70% of the captures, masked shrews 25%, meadow voles 2%, vagrant shrews 2%, pygmy shrews 0.5%, and northern bog lemmings 0.2% of the total captures.

In 1977, the mature crushed site had the highest diversity rating (1.185), the black spruce crushed site had the lowest rating at 0.244 (Table 4). The mature crushed and black spruce uncrushed sites each had five species represented. Four species were found in the mature uncrushed and birch-spruce crushed sites. Only two species were present in the birch-spruce uncrushed and black spruce crushed sites.

In 1978, the diversity ratings were higher in the Willow Lake area than the Moose Research Center or Mystery Creek areas (Table 4). Diversity ratings in 1978 were lower than in 1977. Crushed sites were generally the most diverse sites. In 1977, the mature crushed site at Willow Lake had the highest diversity rating found during this study. Crushing increased species diversity by over 40% in 7 out of 13 comparisons between crushed and uncrushed habitat types. Crushing decreased

TABLE 4. Species diversity of mammals according to the Shannon-Wiener Information Measure.

Site	Area and Date Sampled: Willow Lake 1977	Willow Lake 1978	Moose Research Ctr. 1978	Site	Mystery Creek 1978
Black spruce crushed	.244	.562	.411	Summer '63* crushed	.110
Black spruce uncrushed	.950	.569	.332	Uncrushed* 'A'	.110
Birch-spruce crushed	.840	.970	.264	Winter '77* crushed	.264
Birch-spruce uncrushed	.593	.298	.117	Summer '77* crushed	.238
Mature crushed	1.185	.783	.234	Winter '78* crushed	.142
Mature uncrushed	.816	.521	.363	Uncrushed* 'B'	.131
All sites	1.010	.675	.299	All sites*	.145

* Black spruce sites

species diversity by 40% in only 2 out of the 13 comparisons.

Red-backed Voles

Red-backed voles were the most common species captured. They comprised 45% of the small mammal community at Willow Lake in 1977. In 1978, the red-backed vole population had increased almost 50%. They accounted for 78% of the captures at the Willow Lake area, 92% of the captures at the Moose Research Center area, and 96% of the captures at the Mystery Creek area.

In 1977, red-backed voles were most abundant in the mature sites and least abundant in the black spruce sites (Table 5). The mature crushed site had the highest average capture rate with 87.5 captures per 1000 trap nights. The black spruce crushed site had the lowest capture rate and was significantly different from all other sites trapped in 1977 with only 2.1 captures per 1000 trap nights. Crushing increased red-backed vole densities by 20% in mature sites and significantly reduced their densities in the birch-spruce and black spruce sites by 55% and 93% respectively (Table 6).

The relative abundance of red-backed voles in various sites in 1978 was similar to 1977. In nearly all areas, the vole densities were lowest in the black spruce crushed and birch-spruce crushed sites when compared to their uncrushed counterparts (Table 5).

TABLE 5. The number and distribution of red-backed voles in each study site.

	Site	Area and Date Sampled: Willow Lake 1977		Willow Lake 1978		Moose Research Ctr. 1978		Mystery Creek 1978	
		No.°	Ave.+	No.	Ave.	No.	Ave.	No.	Ave.
40.7	Black spruce crushed	2	2.1	30	41.7	30	62.5	26*	56.3*
55.6	Black spruce uncrushed	30	31.2	29	40.3	35	72.9	37.5**	78.1**
42.0	Birch-spruce crushed	27	28.1	33	45.8	25	52.1		
76.3	Birch-spruce uncrushed	59	61.5	62	86.1	39	81.2		
106.3	Mature crushed	84	87.5	57	79.2	73	152.1		
85.07	Mature uncrushed	69	71.9	87	120.8	30	62.5		
	All sites	271	47.0	298	68.0	232	80.6	181	62.8

° Actual number of captures.
+ Average of captures per 1000 trap/nights.
* Average of four crushed sites.
** Average of two uncrushed sites.

TABLE 6. A ranking of sites in each area according to the density of red-backed vole populations during all trapping periods within each year.

Area and Date Sampled	Most Abundant			Least Abundant		
Willow Lake 1977	mature crushed	mature uncrushed	birch-spruce uncrushed	spruce uncrushed	birch-spruce crushed	spruce crushed
Willow Lake 1978	mature uncrushed	birch-spruce uncrushed	mature crushed	birch-spruce crushed	spruce crushed	spruce uncrushed
Moose Research Ctr. 1978	mature* crushed	birch-spruce uncrushed	spruce uncrushed	spruce crushed	mature & uncrushed	birch-spruce crushed
Mystery Creek 1978°	uncrushed 'A'	uncrushed 'B'	winter '78 crushed	summer '77 crushed	winter '77 crushed	summer '63 crushed

NOTE: Study sites that are underlined by the same line are not significantly different from one another at P.05 as compared by Duncan's new multiple-range test.

* The mature crushed site was significantly different from all sites in the Fall 1978.
° All sites at Mystery Creek are black spruce.

Trapping results indicated that the longer an area had been crushed, the lower the red-backed vole population. In the Mystery Creek area, the lowest trapping success was in the black spruce, summer 1963 crushed site (39.6 captures per 1000 trap nights). All of the black spruce crushed sites at Mystery Creek had lower trapping success than the black spruce uncrushed sites located there (Table 5).

The mature sites had the highest red-backed vole densities in 1978 as they did in 1977. At the Moose Research Center area, the mature crushed site had a significantly higher vole population than all other sites in that area (Table 6). The mature uncrushed site at Willow Lake was significantly higher than any other site in the area. The mature crushed site at Willow Lake was the only site where the population level was lower than the 1977 level.

Capture rates in 1978 were higher than in 1977. The average trapping success at Willow Lake was 47 red-backed voles per 1000 trap nights in 1977 and 68 red-backed voles per 1000 trap nights in 1978. The Moose Research Center area had the highest trap success in 1978 with an average of 80.6 captures per 1000 trap nights. The Mystery Creek area had the lowest average in 1978 with 62.8 captures per 1000 trap nights (Table 5).

Sex ratios of red-backed voles: The sex ratios of red-backed voles varied between periods and sites. The mature sites were the only ones to show significant differences from the expected 1:1 ratio of males and females

in 1977. The mature uncrushed site had a higher percent of females [X^2-4.14, $P<0.025$] while the mature crushed site had a higher percent of males [X^2=5.76, $P<0.025$], (Table 7). Most of the other sites tended to show a higher percentage of males but not significantly. The percentage of males in all sites during 1977 averaged 59%.

The red-backed vole population in 1978 again had a slightly higher percentage of males. The percentage of males in all sites and areas averaged 57%. The black spruce uncrushed 'B' site at Mystery Creek was the only site that was significantly different from a 1:1 sex ratio [X^2=5.45,$P<0.025$].

Age structure of red-backed vole populations: The age structure of the red-backed vole population in each site was related to its relative density. The higher the density the more immatures the population seemed to have. In 1977, the mature sites had the highest percentage of immatures and the black spruce sites had the lowest percentage of immatures. In 1978, crushed sites at the Willow Lake area had a lower percentage of immatures than their uncrushed counterparts. At the Moose Research Center area, the mature crushed site had the highest percentage of immatures of any site at any time. It also had the highest red-backed vole density of any site sampled. The Moose Research Center area had the highest overall average of immatures in the population, as well as the highest red-backed vole densities of any area. At the Mystery Creek area, the two black spruce uncrushed sites had a higher percentage of immatures than the black spruce

TABLE 7. Percentage of males and immatures in the red-backed vole population in each site.

Site	Area and Date Sampled: Willow Lake 1977		Willow Lake 1978		Moose Research Ctr. 1978		Site	Mystery Creek 1978	
	%M°	%I+	%M	%I	%M	%I		%M	%I
Black spruce crushed	100	50	57	70	61	86	Summer '63* crushed	50	75
Black spruce uncrushed	52	55	73	91	57	78	Uncrushed* 'A'	63	97
Birch-spruce crushed	37	60	42	75	62	69	Winter '77* crushed	52	68
Birch-spruce uncrushed	63	64	54	81	54	82	Summer '77* crushed	66	74
Mature crushed	63	90	54	81	62	98	Winter '78* crushed	48	79
Mature uncrushed	37	84	55	85	48	84	Uncrushed* 'B'	71	90

° Percent of males in the red-backed vole population.
+ Percent of immatures in the red-backed vole population.
* Black spruce sites.

crushed sites. The two uncrushed sites had a higher relative density of voles compared to their crushed counterparts.

Uterine scars and embryos in females: The average number of embryos and uterine scars per mature red-backed vole female was used as a relative index of reproduction in each site (Table 8). Significant differences were not detected between sites due to limited sample sizes and the large variation between females. At the Willow Lake area in 1977, the average number of scars and embryos was 9.3. In 1978, the averages were 10.8 at Willow Lake, 11.3 at the Moose Research Center, and 12.2 at the Mystery Creek area. One mature female did not have scars or embryos. The largest number of embryos and scars found in one female was 20. This particular animal was the largest (151 mm long) of any female red-backed vole captured. The large number of scars indicated that three litters had been produced rather than the normal two.

Breeding in red-backed voles starts the first of May and ends by late September. In this study, males were scrotal and the vaginal orifice was perforate in females by May 5th (embryos hadn't formed yet). By late September, males were no longer scrotal and females did not have embryos present.

Meadow Voles

Meadow voles were usually captured in disturbed sites. Preliminary trapping in July 1977 at the Marathon Road crushed

TABLE 8. Average number of uterine scars and/or embryos per mature red-backed vole female.

Site	Area and Date Sampled: Willow Lake 1977	Willow Lake 1978	Moose Research Ctr. 1978	Site	Mystery Creek 1978
Black spruce crushed	0	12.0	13.0	Summer '63* crushed	11.2
Black spruce uncrushed	8.6	6.0	17.5	Uncrushed* 'A'	0
Birch-spruce crushed	7.1	10.6	10.3	Winter '78* crushed	15.6
Birch-spruce uncrushed	9.5	8.0	9.3	Summer '77* crushed	11.2
Mature crushed	9.1	11.5	15.0	Winter '78* crushed	8.5
Mature uncrushed	9.9	12.6	7.0	Uncrushed* 'B'	9.0

* Black spruce sites.

site resulted in the capture of only meadow voles. Trapping at the Willow Lake area in 1977 also resulted in the capture of meadow voles. The mature crushed site had the largest number of captures with 28. Meadow voles were also caught in the birch-spruce crushed site and the black spruce uncrushed site, but were rare (two and one captures, respectively).

In 1978, meadow vole captures were rare. At the Marathon Road crushed site, no meadow voles were captured even though small mammal sign was abundant and there were many tunnels and droppings remaining from the previous winter. Only two meadow voles were captured at the Willow Lake mature crushed site and only two were caught at the black spruce, summer 1963 crushed site in the Mystery Creek area. No other sites had meadow voles present in 1978.

Masked Shrews

Masked shrews were common in all sites in 1977. Generally there were no significant differences in the relative densities of masked shrews between sites (Table 9). The number of shrews was significantly lower [$t=4.6$, $P<0.025$] in 1978 than in 1977 (Table 10). In 1977, there was an average of 45 masked shrews captured per 1000 trap nights. In 1978, at the Willow Lake area, only 14.6 shrews were captured per 1000 trap nights. The Willow Lake area had the largest masked shrew population with the Mystery Creek area having the smallest. In 1978, masked shrews were always more common in the crushed habitat types compared to their

TABLE 9. A ranking of sites in each area according to the density of masked shrew populations during all trapping periods within each year.

Area and Date Sampled	Most Abundant					Least Abundant
Willow Lake 1977	mature crushed	birch-spruce crushed	spruce uncrushed	mature uncrushed	spruce crushed	birch-spruce uncrushed
Willow Lake 1978	mature crushed	mature uncrushed	spruce crushed	spruce uncrushed	birch-spruce crushed	birch-spruce uncrushed
Moose Research Ctr. 1978	spruce crushed	spruce uncrushed	mature crushed	mature uncrushed & crushed	birch-spruce	birch-spruce uncrushed
Mystery Creek 1978°	summer '77 crushed	winter '77 & crushed	uncrushed 'A' &	uncrushed 'B' & crushed	winter '78	summer '63 crushed

NOTE: Study sites that are underlined by the same line are not significantly different from one another at P.05 as compared by Duncan's new multiple-range test.

° All sites at Mystery Creek are black spruce.

TABLE 10. The number and distribution of masked shrews in each study site.

Site	Area and Date Sampled							
	Willow Lake 1977		Willow Lake 1978		Moose Reserach Ctr. 1978		Mystery Creek 1978	
	No.°	Ave.+	No.	Ave.	No.	Ave.	No.	Ave.
Black spruce crushed	28	29.2	10	13.9	5	10.4	1.2*	2.5*
Black spruce uncrushed	48	50	10	13.9	4	8.3	1**	2.1**
Birch-spruce crushed	51	53.1	9	12.5	2	4.2		
Birch-spruce uncrushed	23	24	6	8.3	1	2.1		
Mature crushed	62	64.6	17	23.6	3	6.2		
Mature uncrushed	47	49	11	15.3	2	4.2		
All sites	259	45	63	14.6	17	5.9	7	2.4

° Actual number of captures.
+ Average of captures per 1000 trap/nights.
* Average of four crushed sites.
** Average of two uncrushed sites.

uncrushed counterparts, but not significantly so. The black spruce crushed site at Willow Lake, 1977, was the only site where crushing reduced masked shrew populations.

In 1977, 94% of the shrews captured were immatures. Of the adults captured, 42% were male and 58% were female. The immatures were not sexed. In 1978, all but two shrews captured were immatures. The two adults captured were both males and were the only shrews captured in the spring. Both of these males were captured in the mature crushed site at Willow Lake.

Embryos in adult females averaged 5.8 per female. The most in a single female was 7. One immature female captured in 1977 had embryos present. Mature females did not have embryos present in late September.

Other Species

Vagrant shrews and pygmy shrews were rare and restricted in their distribution throughout this study. Vagrant shrews were the most abundant and widespread of the two. More vagrant shrews were caught in crushed sites than uncrushed sites. In 1977 and 1978, at the Willow Lake area, 11 were caught in the mature crushed site, 6 in the mature uncrushed site, and 9 in the birch-spruce crushed site. In 1978, all but one of the vagrant shrews captured were in the Willow Lake area. One vagrant shrew was caught in the mature uncrushed site at the Moose Research Center.

Pygmy shrews were most abundant in the Willow Lake area and were generally restricted to uncrushed sites. In two summers of trapping at Willow Lake, three were captured in the black spruce uncrushed site, two in the mature uncrushed site, and one in the birch-spruce crushed site. One pygmy shrew was captured in the mature crushed site at the Moose Research Center.

During fall trapping at Marathon Road, all three species of shrews (masked, vagrant, and pygmy) were caught in both the burned, crushed and mature uncrushed sites. Masked shrews were the most abundant and pygmy shrews were the least abundant.

Food Habits

The food habits of voles caught in the Willow Lake area during the summer of 1977 were examined by microscopic analysis. Data were recorded as the percentage of food items in the vole populations diet in each site. Food items that occurred rarely were not included in the table.

Mushroom caps, endogone[1], berries, lichens, and insects were the most common foods used by red-backed voles in the Willow Lake area. Data indicates that the food items used in each site were similar but the relative amounts used varied from site to site (Table 11).

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[1]Endogone is a hypogeous fungus that is reported to be an important small mammal food throughout North America (Bakerspigel 1956, Schloyer 1976).

TABLE 11. Percentage of food items in vole diets for all periods at Willow Lake 1977.

Species	Number Examined	Site	Food Item						
			Berry	Mushroom	Endogone	Moss	Lichen	Insect	Grass
Red-backed voles	2	black spruce crushed	43	50	3	0	0	5	0
	21	black spruce uncrushed	16	31	8	8	13	10	3
	19	birch-spruce crushed	12	11	40	0	19	4	1
	26	birch-spruce uncrushed	27	27	14	4	8	13	3
	25	mature crushed	4	16	33	6	11	10	6
	21	mature uncrushed	10	37	9	6	7	13	4
	114	all sites	14	25	22	5	11	10	3
Meadow voles	19	all sites	0	0	20	15	1	1	42

Meadow voles feed almost exclusively on grass (42%), with endogone and moss comprising the bulk of the other foods used. Mushrooms and berries were not present in the diet. Insects and lichens occurred rarely (Table 11).

Not included in table 11 is data resulting from spring trapping conducted in 1978 at Willow Lake, the Moose Research Center, and Mystery Creek. Stomachs from voles caught in these areas were examined for presence of lowbush cranberries. Many berries were still present during the spring of 1978 and were common in all of these areas. It was evident that cranberries were heavily used in the spring and possibly throughout the winter. At Willow Lake, 20 out of 39 voles had berries present; the Moose Research Center had 28 out of 50; and in the Mystery Creek area, at least 8 out of 15 voles had berries present.

DISCUSSION

Vegetation

The crusher program was designed to simulate the effect of the wildfires which produced vegetation types that resulted in large moose populations on the Kenai Peninsula (Sarber 1944, Lutz 1960, Spencer and Hakala 1964, Oldemeyer 1978). The program seems to succeed in several respects and fail in others. The immediate effect of crushing on all habitat types was to eliminate standing vegetation, increase ground debris, and stimulate browse suckering (Oldemeyer 1978). What crushing failed to do was turn the standing vegetation into an easily available nutrient source for new growth and prepare a seed bed for the introduction of new early stage species.

The amount of browse that grew back in a site seemed to be dependent on the habitat type and area crushed. Vegetative data indicates that the higher the percentage of browse species in an area before crushing, the better the response after crushing. This suggests that vegetative and not seed reproduction is responsible for most of the browse response in treated areas. The amount of aerial debris at Willow Lake indicates the relative productivity of each site before the 1947 burn. Aerial debris as measured for this study is fire-killed black spruce and birch. As table 1 shows, the birch-spruce sites had more aerial debris than the black spruce sites.

As vegetation in these areas grew back, the birch-spruce sites remained more productive. This is true for disturbance by crushing or fire, indicating that disturbance does not alter the relative productivity of each site.

The positive correlation between high aerial debris and high shrub densities on one hand and the amount of browse produced before and after crushing on the other suggests a 'what you see is what you get' philosophy. This philosophy was discussed by investigators studying the response of vegetation in the 1947 burn (US Dept. of Interior, 1950, 1952, Spencer and Hakala 1964). They suggested that certain areas might never produce a high density of browse species because of soil characteristics and a poor seed source for browse production. A particular habitat type apparently has certain characteristics that determine the plant species present and their densities. Fire or any disturbance may temporarily alter the plant stage but basically species and their relative densities do not fluctuate greatly.

It was not the purpose of this study to determine the effects of crushing on vegetation. Vegetation types used in this study were described to give a general impression of the habitats in which small mammals live. The results and discussion that has been presented on vegetation is based on limited information. For a more detailed report on vegetation response to crushing, refer to Oldemeyer (1978).

Species Diversity of Small Mammals

Kirkland (1977) and Martell and Radvanyi (1977) indicated that disturbance in forests tended to increase the species diversity of small mammals. Tree crushing generally did increase the species diversity of small mammals. In 1977, the diversity ratings were higher than in 1978 because red-backed vole populations increased in 1978 while other species decreased. The increased diversity ratings of crushed sites in 1977 compared to their uncrushed counterparts was primarily due to populations of other species becoming more abundant while red-backed vole populations declined. In 1978, the higher diverstiy ratings of crushed sites was primarily due to red-backed vole populations decreasing rather than other species increasing. Basically, the species diversity ratings of all sites was dependent on the ratio of red-backed voles to other species. Generally, when red-backed vole populations decreased the diversity rating increased. An exception to this was in 1977 at the mature crushed site in the Willow Lake area. In this site, the red-backed vole population increased but so did three other species and the result was the highest species diversity rating of any site studied during this project.

Red-backed Voles

Red-backed voles were by far the most abundant species captured in this study. They are reportedly common through-

out boreal forests (Hall and Kelson 1959, Douglass 1977b). Studies suggest that, while they are not restricted to a particular habitat type, they do reach their highest population densities in mature forest types (Ahlgren 1966, Gashwiler 1970, Turner et al. 1975, Douglass 1977a). This theory was supported during this study. Undisturbed mature forest types at Willow Lake tended to have the highest red-backed vole densities.

Red-backed voles in disturbed sites are usually associated with debris (Gunderson 1959, Krefting 1974, Richens 1974, Martell and Radvanyi 1977, Miller and Getz 1977). This study showed a strong relationship between protective cover in the form of aerial debris and high relative population densities. Vole numbers increased in sites where crushing increased protective cover. In sites where cover was decreased, vole numbers decreased. Vegetative data suggests that the voles' food supply was not severely affected by crushing and the immediate response of the vole population was due to cover rather than food requirements.

Red-backed voles are not associated with disturbed sites and usually decrease with most types of disturbance (Douglass 1977a, Martell and Radvanyi 1977). This is thought to be due to destruction of the food supply as well as a decrease in cover (Ahlgren 1966). One study did show that the vole population first increased with logging disturbance, then began to decrease after three years (Martell and Radvanyi

1977). The increase was thought to be a result of increased cover. As the plant species changed, the preferred food species declined resulting in the decrease of red-backed vole densities. This is believed to have occurred in the Willow Lake mature crushed site between 1977 and 1978. At first, the red-backed vole population was provided with a huge increase in protective cover with almost no damage to the food supply. The population increased rapidly. As plant succession changed, the amount of available food decreased and the population declined. The data from the Marathon Road area and Mystery Creek area indicated that sites crushed 6 and 15 years ago and had lower red-backed vole densities than recently crushed sites.

Another explanation of this pattern is that other species move into the disturbed sites and drive out the red-backed voles. Many studies have shown that meadow voles and red-backed voles tend to exclude each other from certain areas (Morris 1969, Turner et al. 1975). Meadow voles are generally associated with disturbed areas or grasslands (Eadie 1953, Getz 1961, Chitty 1967, Grant 1971), while red-backed voles are associated with undisturbed mature forest sites. Meadow voles disappeared from the Marathon Road area during the winter of 1977-78. The following year, only red-backed voles and shrews were captured. Turner et al. (1975) suggested that meadow voles may prevent red-backed voles from using some areas because of the aggressive behavior between these two species.

The trapping results on Marathon Road tended to support the competitive exclusion theory, although at the Willow Lake mature crushed site, meadow voles and red-backed voles were both present. It is possible that there were microhabitats (Dueser and Shugart 1978) formed by disturbance within this site that was supporting a small meadow vole population. In general, results from this study support the competitive exclusion theory between meadow and red-backed voles. (Competitive exclusion may be an inappropriate term since the food habits and cover requirements of the two species are different. Behavioral intolerance may better describe the separation of meadow and red-backed voles.) It is doubtful that meadow voles were responsible for the reduction in the red-backed vole population in the mature crushed site at Willow Lake since meadow voles were rare in 1978. It is much more reasonable to assume that the early successional plant stages are less able to support high red-backed vole populations than undisturbed sites.

The winter and spring of 1977-78 were favorable for vole survival (Merritt and Merritt 1978). Snow in the fall of 1977 came quickly and stayed on the ground to provide insulation from extreme temperatures. There were no appreciable thaws until spring. Spring break-up was mild with a slow thaw and little flooding. The berry and mushroom crops during the summer of 1977 were very abundant. There were still many berries remaining on the ground during the spring

thaw and were extensively used by the red-backed voles. The mild winter, abundant food supply, and wetter summer conditions of 1978 seemed to allow the red-backed vole population to expand. The very high vole population in 1978 may have even masked some of the true effects of crushing. Voles may have overflowed into marginal habitats (Errington 1946) that they would not normally select.

Several aspects of the population structure of red-backed voles may have been indicators of population densities and trends. It has been suggested that survival of the young is the most important factor influencing the relative population densities of mammals (Frank 1957, Morris 1969, Caughley 1970, Getz 1970). Data from this study supports that theory. The highest vole population almost always had the highest percentage of immatures in the catch. There was an apparent increase in red-backed voles from 1977 to 1978. The 1978 population was comprised of more immatures than the 1977 population.

Some studies have suggested that the sex ratio of a population may indicate whether its density is increasing or decreasing (Pitelka 1957, Hansson 1978). Other studies have reported that the sex ratio has no relation to population densities (Tevis 1956, VanVleck 1968). Almost all studies have shown that trapping is biased in favor of males due to behavioral factors (Davis 1956, Pitelka 1957, Marten 1972).

Trapping results from this study tended to give some support to each theory. In 1977, all sites at Willow Lake except the mature uncrushed and birch-spruce crushed sites showed a majority of males in the population. Only the mature crushed site was significantly different from a 50:50 sex ratio with 63% of the population being male. The mature crushed site had a lower vole population during 1978 than 1977, which supports a theory that a high percent of males in the population indicates a decreasing population.

The mature uncrushed site had a significant excess of females and this population increased during 1978. Reportedly, there is a higher percentage of females in unburned sites (Lidicker 1975, Buech et al. 1977, Hansson 1978). At Willow Lake and the Moose Research Center, the mature uncrushed sites did tend to have a higher percentage of females than males. To discount this theory, there is also the fact that the birch-spruce crushed site at Willow Lake in 1977 and 1978 also had a surplus of females, but not significantly so. This population did increase in 1978, but then so did all the other sites at Willow Lake, except the mature crushed site. In most cases, the high ratios of either sex are probably due to experimental variation and behavioral differences. At significant levels the higher ratio of one sex may suggest a relative population level or trend.

The sex and age of small mammals that tend to repopulate disturbed sites has been commented on by many observers.

Some suggest that pregnant females are the primary immigrants into low density areas (Lidicker 1975). Others are inclined to believe that young adults or males repopulate new habitats first (LoBue and Darnell 1959, Morris 1969, Fuller 1977).

Results from this study show that recently repopulated sites contain the same relative proportions of males and immatures as found in other sites. The black spruce crushed site at Willow Lake was an excellent example for determining when most of the dispersal of small mammals takes place. In 1977, the black spruce crushed site was nearly void of life. Both voles and birds were rare. In 1978, during the August trapping period, many birds were captured indicating vegetation in the site had responded enough to support an animal population (Appendix B). However, voles were still scarce. A month later, fall trapping indicated that voles had repopulated the area and were at fairly high levels. The population had a normal composition of males and immatures.

This information shows two important concepts in vole population dynamics. Voles disperse in the fall (August or early September), and all age classes and sexes move into an area. Late September or fall dispersal is noted commonly throughout the literature (Errington 1946, Ellison 1975).

Red-backed voles in Alaska are believed to have winter and summer use areas (West 1977). Spring trapping tended to support this concept. More voles were caught in sites that had thick moss and/or vegetative cover that provided a

proper subnivean environment (Coulianos and Johnels 1962, Fuller et al. 1969). Spring densities were not strongly correlated to late fall densities. This could have been due to small sample sizes in spring or voles having different food and cover requirements at different times of the year. Crushing did affect red-backed voles more in the spring of the year than the fall.

Red-backed voles did not show any major differences in the number of embryos or scars per female in relation to site, area, or relative population densities. Previous work on red-backed voles and other microtines has also suggested that there aren't usually differences in production per female at various population densities (Tevis 1956, Douglass 1977b). Variation between females and limited sample sizes in this study do not allow for any defendable statements. However, embryo and scar counts from Willow Lake were slightly greater in 1978 than in 1977 and there was a higher percentage of immatures and a relatively higher red-backed vole population in 1978. There was also a higher embryo and scar count at the Moose Research Center area than at the Willow Lake area, and the Moose Research Center did have a higher percentage of immatures in the population and a higher relative population of red-backed voles. These were the only instances found during this study where the increased reproduction per female may have resulted in an increased population. Frank (1957) and Pitelka (1957) also indicated that production per

female may increase in an increasing population. To fully support this idea would require much more data on the production per female than was obtained during this study.

Being the most abundant species captured, the red-backed vole becomes the most important, both in terms of its role as an important prey item and its possible influence on the type of vegetation coming back in treated areas. Red-backed voles are important prey species for many predators, both avian and mammalian (Elton 1942, Ozoga and Harger 1966). It is well known that some predator populations are dependant on prey densities (Pearson 1964, 1966, 1971, Maher 1967, Fitzgerald 1977). The fox-vole cycles and lemming-raptor cycles are particularly striking examples of this relationship in northern climates (Elton 1942, Pitelka et al. 1955). It is assumed that whatever is good or bad for the vole population will have a direct effect on their predators' populations (Appendix D).

Evidence of mass destruction of crops, forests, and natural vegetation by small mammals is common throughout the literature (Elton 1942). Most of the early research on small mammals was undertaken in the hopes of finding ways to stop this damage. Many papers have dealt with the problems of mice affecting the type of vegetation coming back in disturbed sites (Sims and Buckners 1973, Pank 1974). In some planting and reseeding programs, success or failure was determined by the extent of damage by rodents. Most of the damage in such programs is done at the seeding stage (Smith and Aldous 1947,

Radvanyi 1966, Gashwiler 1969, Martell and Radvanyi 1977). Radvanyi (1970) reported that the success of a white spruce seeding program doubled by spreading seeds in the winter instead of the summer. Increased consumption of seeds by small mammals in the summer was believed to be the reason for the seasonal difference in the success of the program.

In the crushed program which is designed to inhibit spruce production and promote browse regrowth, seasonal differences in the destruction of seeds becomes very important. Summer crushing instead of winter crushing could theoretically reduce spruce reproduction and greatly increase the overall effectiveness of the program, that is, if small mammals on the Kenai Peninsula are important seed predators.

In analysis of red-backed vole food habits, it was determined that they primarily feed on fruits, lichens, and mushrooms during the summer. It has been proposed that in the winter, voles feed on seeds that have been gathered during the summer (Gashwiler 1970, Golley et al. 1975, Merritt and Merritt 1978). Red-backed voles have been known to eat up to 232 white pine seeds per day, or 2,000 white spruce seeds per day (Wagg 1963). Most research, however, indicates that red-backed voles are not normally seed eaters and feed primarily on fruits, lichens, and mushrooms (Stebbins 1976, Buech et al. 1977, Martell and Radvanyi 1977). If predation on seeds does take place, it is probably limited to the winter and has very little effect on the seed crop as a whole. On

the Kenai Peninsula, it is doubtful that red-backed voles have any influence on the densities or type of vegetation coming back in treated areas since they did not seem to eat spruce seeds to any extent. In most northern climates, it has been shown that red-backed voles have little effect on reforestation of disturbed areas (Hansson 1974, Buech et al. 1977).

Meadow Voles

Meadow voles are primarily grassland specialists (Getz 1961, Batzli 1971, Grant 1971), and it is no surprise that they were not common or abundant in this study. Meadow voles are generally associated with various types of disturbance (Douglass 1977a). Of 36 meadow voles captured in this study, 35 were caught in sites that had been disturbed. The relative abundance of meadow voles decreased dramatically in 1978 when compared to 1977. The reason for this decline can only be speculated. Red-backed voles are known to have high water requirements (Gunderson 1959). It is possible that the wetter summer of 1978 favored red-backed voles and meadow voles were driven out of the study area. Meadow voles are known to have dramatic fluctuations in their population levels and it appeared that such a decline occurred in the winter of 1977-78. Vole tunnels and sign were abundant at Marathon Road in the spring of 1978 although no voles were captured at that time. (Meadow voles had been the only

species captured there in 1977.) In the fall of 1978, meadow voles were not captured either at Marathon Road or at the Willow Lake mature crushed site. The rapid disappearance of meadow voles from sites where they had been common is noted throughout the literature (Elton 1942, Batzli 1971). The cause for these declines is unknown.

The food habits and capture records show that meadow voles are specialists and dependant on grass for food and cover. Grass composed most of their diet. Zimmerman (1965) reported that meadow voles rarely used berries and mushrooms. This was also true in this study. Only endogone and moss had any importance in the diet besides grass. Meadow voles, like red-backed voles, were not using coniferous seeds as a food source.

Meadow voles need protective cover in the form of thick grass stands (LoBue and Darnell 1959). Pure grass stands only occurred in the mature crushed site at Willow Lake and in the crushed, burned site at Marathon Road. These were the only two sites where meadow voles were caught in any appreciable numbers.

It has been suggested that if meadow voles were abundant enough, they could affect vegetation coming back in treated areas. It has been shown that their presence in various disturbed areas has resulted in destruction to both seeds and seedlings (Wagg 1963, Golley et al. 1975). Information from this study indicates that they did not reach very high densi-

ties in 1977 or 1978 and were not using coniferous seeds for food; thus, it is doubtful that meadow voles could have any effect on the type of vegetation coming back into treated areas. The vegetation types needed to support high populations of meadow voles are not common on the Kenai Peninsula.

Masked Shrews

Masked shrews are common throughout boreal forests and are commonly associated with red-backed voles (Buech et al. 1977, Martell and Radvanyi 1977). Other work on small mammal populations has shown masked shrews to be the only other abundant species besides red-backed voles (Fuller et al. 1974, Richens 1974, Ramirez 1976). Masked shrews, like red-backed voles, aren't usually associated with any particular habitat types (Brown 1967, Ellison 1970). In 1977, masked shrews were only slightly less abundant than red-backed voles. Masked shrews were found in every habitat type. Habitat disturbance affected shrews much less than it did voles during 1977 and 1978. The lack of response by shrews to habitat disturbance is supported in the literature (Kirkland 1977). In two summers of trapping, the only significant differences were between the very high shrew densities in the mature crushed and birch-spruce crushed sites and the low densities in the black spruce crushed and birch-spruce uncrushed sites at Willow Lake in 1977.

Masked shrew populations have been reported to fluctuate greatly through time (Woolfenden 1959, Martell and Radvanyi

1977). This is supported by trapping information during this and other studies (Appendix E). Masked shrews were abundant in 1977 and found in all sites during 1977 and 1978. In 1978, the shrew population was much lower than in 1977. The low spring trapping success in 1978 (only two shrews captured), and the fact that all of the masked shrews captured in the fall of 1978 were immatures indicates that during the winter of 1977-78, a drastic reduction took place in the shrew population. This is believed to be the reason for the decline in the trapping success in 1978.

Unlike red-backed voles, shrews are not thought to be an imporatnt prey species for small mammal predators (Ozoga and Harger 1966). The different rates of predation on each of these species may be a reason why disturbance of vegetation and consequent loss of cover affects shrews much less than it does voles.

Other Species

Other species of shrews are usually found at lower densities than masked shrews (Richens 1974, Buech et al. 1977). This was also the case in this study. Masked shrews were much more abundant than either vagrant or pygmy shrews in both 1977 and 1978. Some authors suggest that various species are associated with different habitat types based on moisture content (Brown 1967, Terry 1978). Masked shrews are associated with moist sites, vagrant shrews with dryer sites, and

pygmy shrews with very damp sites. This was supported in this study. Although vagrant shrews were associated with slightly drier sites, and pygmy shrews were associated with damp sites, it must also be noted that the sample sizes of these species were small and subject to experimental error. Trapping at Marathon Road showed that these three species were found in the same sites. More vagrant shrews were caught in the drier crushed, burned site, but not significantly so. Vagrant and pygmy shrews are probably associated with micro-habitats (Dueser and Shugart 1978) that are found throughout more general habitat types. These shrew species are probably at very low densities throughout most habitat types.

CONCLUSIONS

The immediate effect of crushing on vegetation is the same for all habitat types. Crushing reduces tree densities, increases ground debris, and increases shrub densities. How quickly vegetation responds depends upon the habitat type and location treated. The kinds and amounts of vegetation that grows back in treated areas also depends on the habitat types and location. Mature hardwood stands produced the most aerial debris and browse regrowth. Black spruce regrowth stands produced the least. Vegetation in the Willow Lake area responded the most favorably to crushing. Vegetation in the Mystery Creek area responded the poorest.

Microhistological analysis of vole food habits show that red-backed voles are generalists and meadow voles are specialists. Red-backed voles primarily fed on fruits, lichens, and fungus. The amount of each food item used varied with availability. Meadow voles fed almost exclusively on grasses. Neither species was using coniferous seeds as a food source, so it is very doubtful that they affect the revegetation of disturbed sites.

Red-backed voles and masked shrews were the most abundant species captured before and after crushing. Red-backed voles were at relatively high densities in 1977 and 1978. Masked shrews were at high densities in 1977 and at low densities in 1978. Other species were at low levels during

both years. When crushing increased aerial debris, small mammal density and diversity increased. When crushing decreased aerial debris, small mammal densities decreased while species diversity increased. Generally, crushing reduced red-backed vole densities, and increased the overall species diversity. Shrew populations were the only small mammal population not seriously affected by crushing.

REFERENCES CITED

Ahlgren, C.E. 1966. Small mammals and reforestation following prescribed burning. J. Forest. 64:614-617.

Bakerspigel, A. 1956. Endogone in Saskatchewan and Manitoba. Amer. J. Botany 43:471-475.

Banks, R.C. 1965. Weight changes in frozen specimens. J. Mammal. 46:110.

Batzli, G.O. 1971. Condition and diet of cycling populations of the California vole Microtus californicus). J. Mammal. 52(1):141-163.

_____. 1975. The role of small mammals in arctic ecosystems; In Small Mammals: their productivity and population dynamics. Cambridge Univ. Press. p. 243-268.

Baumgartner, L.L., and A.C. Martin. 1939. Plant histology as an aid in squirrel food-habit studies. J. Wildl. Manage. 3(3):266-268.

Beer, J.R. 1964. Bait preferences of some small mammals. J. Mammal. 45:632-634.

Bitterlich, W. 1947. Die Winkelzahlmessung. (Measurement of basal area per hectare by means of angle measurement). Allg. Forst und Holzwirtsch. Ztg. 58:94-96.

Bock, C.E., and J.F. Lynch 1970. Breeding bird populations of burned and unburned conifer forest in the Sierra Nevada. The Condor. 72:182-189.

Brown, L.N. 1967. Ecological distribution of six species of shrews and comparison of sampling methods in the central Rocky Mountains. J. Mammal. 48:617-623.

Buech, R.R., K. Siderits, R.E. Radtke, H.C. Sheldon, and D. Elsing. 1977. Small mammal populations after a wildfire in northeast Minnesota. USDA Forest Service, Research Paper NC-151. North Central Forest Experiment Station. 8pp.

Caughley, G. 1970. Eruption of ungulate populations, with emphasis on Himalayan thar in New Zealand. Ecology. 51:53-72.

Chitty, D. 1967. The natural selection of self-regulatory behavior in animal populations. Proc. Ecol. Soc. Aug. (2):51-78.

Coulianos, C.C., and A.G. Johnels. 1962. Note on the subnivian environment of small mammals. Arkiv Zoologi. 15:363-370.

Davis, D.E. 1956. Manual for small mammal studies. Library Congress Catalog Card No. 57-7458. 82pp.

Dearden, B.L., R.M. Hansen, and R.E. Pegau. 1972. Plant fragment discernibility in caribou rumens. Proc. First Inter. Reindeer and Caribou Symp. Biol. Papers Univ. of Alaska. Report No.1:257-277.

Douglass, R.J. 1977a. Effects of a winter road on small mammals. J. Appl. Ecol. 14:827-834.

_____. 1977b. Population dynamics, home ranges and habitat association of the Yellow-cheeked vole Microtus xanthognathus in the Northwest Territories. Can. Field-Nat. 91:237-247.

Dueser, R.D. and J.H. Shugart, Jr. 1978. Microhabitats in a forest-floor small mammal fauna. Ecology. 59(1): 89-98.

Dusi, J.L. 1949. Methods for the determination of food habits by plant microtechniques and histology and their application to cottontail rabbit food habits. J. Wildl. Manage. 13(3):295-298.

Eadie, W.R. 1953. Response of Microtus to vegetative cover. J. Mammal. 34(2):263-264.

Ellison, L.N. 1970. Small mammal study in Swanson River 1969 burn. Unpublished data on file KNMR, Kenai, Alaska. 3pp.

_____. 1975. Density of Alaskan spruce grouse before and after fire. J. Wildl. Manage. 39(3)468-471.

Elton, C.H. 1942. Voles, Mice, and Lemmings: Problems in population dynamics. Oxford Univ. Press. 496pp.

Errington, P.L. 1946. Predation and vertebrate populations. Quart. Rev. Biol. 21(2):144-177, 21(3):221-245.

Fitzgerald, B.M. 1977 Weasel predation on a cyclic population of the montane vole Microtus montanus in California. J. Anim. Ecol. 46:367-397.

Frank, F. 1957. The causality of microtine cycles in Germany. J. Wildl. Manage. 21(2):113-121.

Fuller, T.K., J. Haney, and S. Minta. 1974. Survey of mammals of the Kenai National Moose Range, Alaska. Unpublished data on file KNMR, Kenai, Alaska.

Fuller, W.A. 1977. Demography of a subarctic population of Clethrionomys gapperi: size and growth. Can. J. Zool. 55:415-425.

_____, L.L. Stebbins, and G.R. Dyke. 1969. Overwintering of small mammals near Great Slave Lake northern Canada. Arctic. 22(1):34-55.

Gashwiler, J.S. 1969. Deer mouse repopulation of a poisoned Douglas-fir clearcut. J. Forest. 67(7):494-497.

_____. 1970. Plant and mammal changes on a clearcut in west-central Oregon. Ecology. 51(6):1018-1026.

Getz, L.L. 1961. Factors influencing the local distribution of Microtus and Synaptomys in southern Michigan. Ecology. 42(1):110-119.

_____. 1970. Influence of vegetation on the local distribution of the meadow vole in southern Wisconsin. Univ. of Conn. Occassional Papers, Biol. Science Series. 1:213-241.

Golley, F.B., K. Petrusewicz, and L. Ryszkowski. 1975. Small mammals: their productivity and population dynamics. Cambridge Univ. Press. 451pp.

Grant, P.R. 1971. The habitat preference of Microtus Pennsylvanicus and its relevance to the distribution of this species on islands. J. Mammal. 52(2):351-361.

_____. 1976. An 11-year study of small mammal populations at Mon't St. Hilaire, Quebec. Can. J. Zool. 54:2156-2173.

Gunderson, H.L. 1959. Red-backed vole habitat studies in central Minnesota. J. Mammal. 40(3):405-412.

Hall, E.R. 1962. Collecting and preparing study specimens of vertebrates. Univ. of Kansas. Miscellaneous Pub. No. 30. 46pp.

_____, and K.R. Kelson. 1959. The mammals of North America. 2 vols. The Ronald Press New York. 1083pp.

Hansson, L. 1974. Small mammal productivity and consumption in spruce forests and reforestation in south Sweden. Oikos. 25:153-156.

Hansson, L. 1978. Sex ratio in small mammal populations as affected by the pattern of fluctuations. Acta. theriologica. 23(10):203-212.

Hooven, E.F., and H.C. Black. 1976. Effects of some clearcutting practices on small mammal populations in western Oregon. Northwest Science. 50(4):189-208.

Kirkland, G.L., Jr. 1977. Responses of small mammals to the clearcutting of northern Appalachian forests. J. Mammal. 58(4):600-609.

Krefting, L.W. 1974. Small mammals and vegetation changes after fire in a mixed conifer-hardwood forest. Ecology. 55(6):1391-1398.

Kulow, D.L. 1965. Elementary point-sampling. West Virginia Univ., Ag. Exp. Station. Cir.116. 24pp.

Lidicker, W.Z., Jr. 1975. The role of dispersal in the demography of small mammals. In Small Mammals: their productivity and population dynamics. Cambridge Univ. Press. p.103-128.

LoBue, J., and R.M. Darnell. 1959. Effect of habitat disturbance on a small mammal population. J. Mammal. 40(3):425-437.

Lutz, H.J. 1960. History of the early occurrence of moose on the Kenai Peninsula and in other sections of Alaska. Alaska Forest Research Center, US Dept. Agr., Misc. Publ. No.1 25pp.

Maher, W.J. 1967. Predation by weasels on a winter population of lemmings, Banks Island, Northwest Territories. Can. Field-Nat. 81(4):248-250.

Martell, A.M., and A. Radvanyi. 1977. Changes in small mammal population after clearcutting of northern Ontario black spruce forest. Can. Field-Nat. 91:41-46.

Martén, G.G. 1972. Censusing mouse populations by means of tracking. Ecology. 53(5):859-867.

McKeever, S. 1961. Relative populations of small mammals in three forest types of northeastern California. Ecology. 42(3):399-402.

Merritt, J.F., and J.M. Merritt. 1978. Population ecology and energy relationships of Clethrionomys gapperi in a Colorado subalpine forest. J. Mammal. 59(3):576-598.

Miller, D.H., and L.L. Getz. 1977. Factors influencing local distribution and species diversity of forest small mammals in New England. Can. J. Zool. 55:806-814.

Morris, R.D. 1969. Competitive exclusion between Microtus and Clethrionomys in the Aspen Parkland of Saskatchewan. J. Mammal. 50(2)L291-301.

Oldemeyer, J.L. 1978. Two year response of woody plants to Letourneau tree crushers on the Kenai National Moose Range. N. Amer. Moose Conf. 14, Halifax, Nova Scotia. 13pp.

Ozoga, J.J., and E.M. Harger. 1966. Winter activities and feeding habits of northern Michigan coyotes. J. Wildl. Manage. 30(4):809-818.

Pank, L.F. 1974. A bibliography on seed eating mammals and birds that affect forest regeneration. Special Sci. Report. Wildlife. No. 174 Washington D.C.

Pearson, O.P. 1964. Carnivore-mouse predation: An example of its intensity and bioenergetics. J. Mammal. 45(2): 177-233.

_____. 1966. The prey of carnivores during one cycle of mouse abundance. J. Animal Ecol. 35(1):217-233.

_____. 1971. Additional measurements of the impact of carnivores on California voles, Microtus californicus. J. Mammal. 52(1):41-49.

Pitelka, F.A. 1957. Some aspects of population structure in the short term cycle of the brown lemming in northern Alaska. Cold Spring Symp. on Quant. Biol. 22:237-251.

_____, P.Q. Tomich, and G.W. Treichel. 1955. Ecological relations of jaegers and owls as lemming predators near Barrow, Alaska. Ecol. Mono. 25(3):85-117.

Pucek, Z., and V.P.W. Lowe. 1975. Age criteria in small mammals. In Small mammals: their productivity and population dynamics. Cambridge Univ. Press. p.55-72.

Radvanyi, A. 1966. Destruction of radio-tagged seeds of white spruce by small mammals during summer months. Forest Sci. 12:307-315.

_____. 1970. Small mammals and regeneration of white spruce forests in western Alberta. Ecology. 51:1102-1105.

Ramirez, P. 1976. Ecology of the wolverine in northwestern Montana. Unpublished data, third annual report. Idaho Coop. Wildl. Research Unit. Univ. of Idaho. Tables 18-20

Rausch, R. 1952. Studies on the helminth fauna of Alaska. XI Helminth parasites of microtine rodents; taxonomic considerations. J. Parasitology. 38(5):415-440.

Richens, V.B. 1974. Numbers and habitat affinities of small mammals in northwestern Maine. Can. Field-Nat. 88:191-196.

Sarber, H.R. 1944. Report of moose studies, National Moose Range, Kenai Peninsula, Alaska. US Fish & Wildl. Serv. Report.

Schloyer, R. 1976. Changes in food habits of Peromyscus manicultus nubiterrae Rhoads on clearcuts in West Virginia. Proceed. Penn. Acad. Sci. 50:78-80.

Sealander, J.A., and D. Jones. 1958. Relative efficiency of different small mammal traps. J. Mammal. 39(1): 215-223.

Sims, J.P., and C.H. Buchners. 1973. The effects of clear-cutting and burning of Pinus banksiana forest on the populations of small mammals in southeastern Manitoba. Amer. Midl. Nat. 90:228-231.

Smith, D.F., and S.E. Aldous. 1947. The influence of mammals and birds in retarding artificial and natural reseeding in coniferous forests in the United States. J. Forest. 43:361-369.

Sparks, D.R., and J.C. Malechek. 1968. Estimating percentage dry weight in diets using a microscopic technique. J. Range Manage. 21(4):261-265.

Spencer, D.L., and J.B. Hakala. 1964. Moose and fire on the Kenai. Proc. Tall Timbers Fire Ecology Conf. 3. 33pp.

Steel, R.G.D., and J.H. Torrie. 1960. Principles and proceedures of statistics. McGraw-Hill Book Co., Inc. 481pp.

Stebbins, L.L. 1976. Overwintering of the red-backed vole at Edmonton, Alberta, Canada. J. Mammal. 57(3):554-561.

Terry, C.J. 1978. Food habits of three sympatric species of Insectivora in western Washington. Can. Field-Nat. 92(1): 38-44.

Tevis, L. Jr. 1956. Responses of small mammal populations to logging of Douglas-fir. J. Mammal. 37:189-196.

Thompson, D.Q. 1955. The role of food and cover in population fluctuations of the brown lemming at Point Barrow, Alaska. Trans. N. Amer. Wildl. Conf. 20:166-176.

Turner, B.N., M.R. Perrin, and S.C. Iverson. 1975. Winter coexistence of voles in spruce forests: relevance of seasonal changes in aggression. Can. J. Zool. 53: 1004-1011.

U.S. Department of Interior. 1950. Narrative report, Kenai National Moose Range, unpublished. Kenai, Alaska.

_____. 1952. Narrative report, Kenai National Moose Range, unpublished. Kenai, Alaska.

_____. 1961. Narrative report, Kenai National Moose Range, unpublished. Kenai, Alaska.

Van Vleck, D.B. 1968. Movements of Microtus pennsylvanicus in relation to depopulated areas. J. Mammal. 49:92-103.

Wagg, J.W.B. 1963. Notes on food habits of small mammals of the white spruce forest. Forest. Chronicle No. 517.

West, S.D. 1977. Midwinter aggregation in the northern red-backed vole, Clethrionomys rutilus. Can. J. Zool. 55: 1404-1409.

Whitney, P. 1976. Population ecology of two sympatric species of subarctic microtine rodents. Ecol. Mono. 46:85-104.

Williams, O. 1962. A technique for studying microtine food habits. J. Mammal. 43(3):365-368.

Wilson, E.O., and W.H. Bossert. 1971. A primer of population biology. Sinauer Assoc. Inc. Sunderland, Mass. 189pp.

Wolff, J.O. 1978. Food habits of snowshoe hares in interior Alaska. J. Wildl. Manage. 42(1):148-153.

_____, and J.C. Zasada. 1975. Red squirrel response to clearcut and shelterwood systems in interior Alaska. USDA Forest Serv. Research Notes. PNW-255:1-7.

Woolfenden, G.E. 1959. An unusual concentration of Sorex cinereus. J. Mammal. 40(3):437.

Zimmerman, E.G. 1965. A comparison of habitat and food of two species of Microtus. J. Mammal. 46:605-612.

APPENDIX

APPENDIX A

A Modified Museum Special Snap Trap

Museum special snap traps were the type of traps used in this project. They are one of the most popular tools used for sampling small mammal communities. They are relatively inexpensive and readily available. Snap traps are also easy to use in the field because they are lightweight and easy to set. The major disadvantage of snap traps is that they are size selective in the kinds of animals caught.

After the first 2,000 trap nights of use, it was evident that although voles were not escaping, smaller mammals such as shrews were. Numerous traps were snapped but empty, many of which had shrew droppings on them. The large number of shrews caught only by the tail, and in some instances, only a piece of the tail remaining in the trap, indicated that many shrews were being missed by the traps. Shrew numbers were obviously underestimated in the catch.

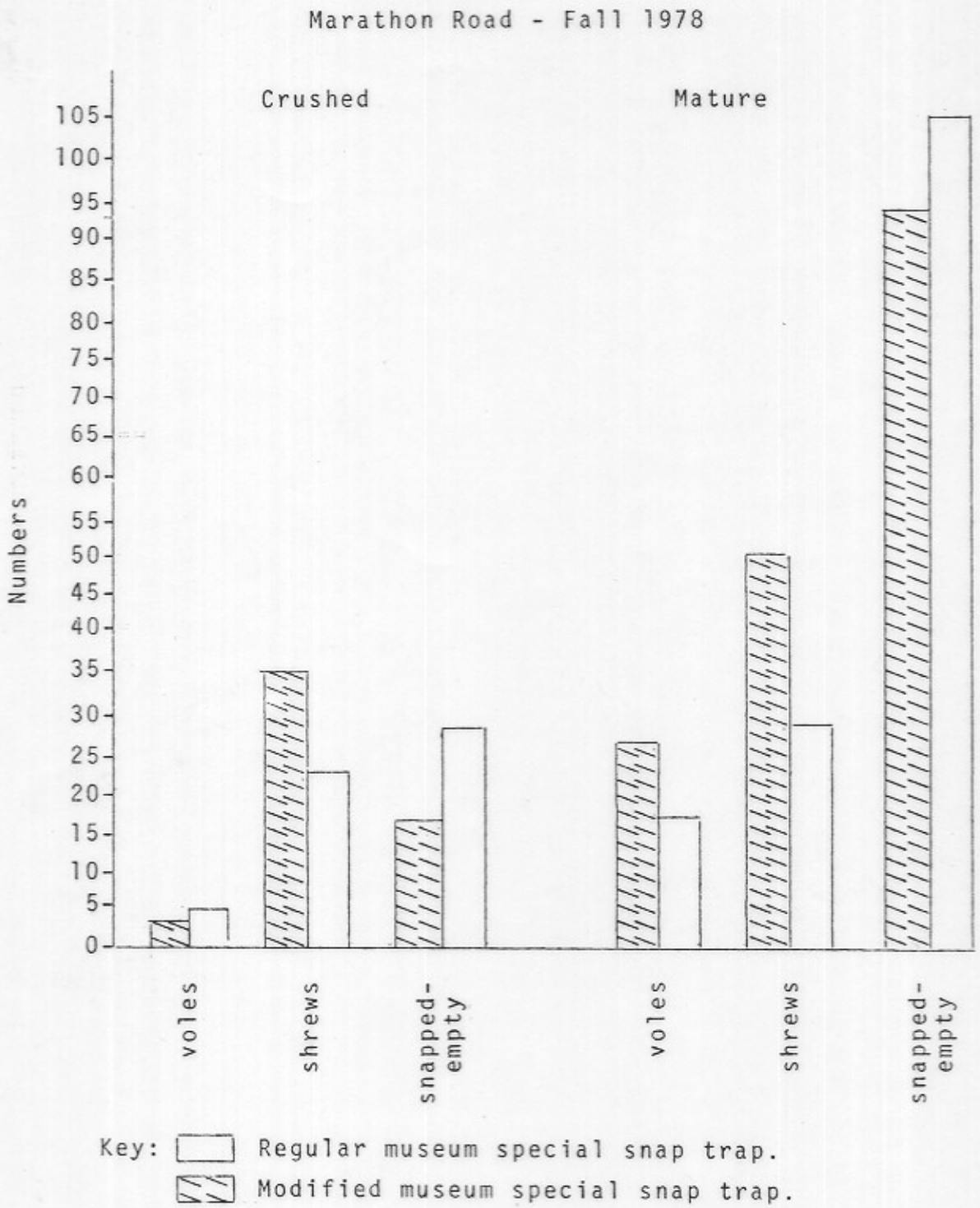
Several other authors have commented that snap traps were ineffective at sampling shrew populations (Sealander and Jones 1958, Brown 1967, Richens 1974). This information led to the modification of the museum special snap trap so that shrews as well as voles could be sampled more effectively.

The traps were modified by placing a small wire (#22 stainless steel wire) across the striker bar. The wire was wrapped around each side of the striker bar and silver sold-

ered in place. When the trap was snapped, the wire passed about 5 mm in front of the trigger. This prevented the striker bar from passing over smaller mammals without catching them.

The museum special snap traps were inexpensive to modify and proved to be very durable. It took less than 16 man-hours to modify 400 traps. The wires held up very well with only one breaking in over 12,000 trap nights of use.

Results from a direct comparison of modified and unmodified traps indicated that the modified trap was a much more effective tool for sampling small mammal communities. The modified traps caught significantly more shrews [$t=7.48, P<0.05$], slightly more voles, and had fewer snapped but empty traps than the unmodified trap (Appendix A. Fig. 1). It was found that the use of the modified traps had three advantages over regular museum special traps: 1. Modified traps reduced the unknown factor associated with a large number of snapped but empty traps (Appendix A. Table 1). 2. Modified traps reduced from 14 (in 1977) to 0 (in 1978) the number of mammals that were unidentifiable to species because only a portion of a tail was left in the trap. 3. Modified traps were more effective at sampling all segments of the small mammal community than were unmodified traps. The increased effectiveness of the modified trap, the low cost of modification, and their durability make this trap a much more efficient tool for use in sampling relative densities of small mammals.



Appendix A. Fig. 1. Comparison of trap success between regular and modified museum special snap traps.

APPENDIX A. TABLE 1. The number of traps that were snapped but empty per 100 trap nights.

Site	Area and Date Sampled			Site	Mystery Creek 1978**
	Willow Lake 1977*	Willow Lake 1978**	Moose Research Ctr. 1978**		
Black spruce crushed	8.6	7.1	1.0	Summer '63° crushed	2.1
Black spruce uncrushed	15.2	10.6	2.5	Uncrushed° 'A'	3.1
Birch-spruce crushed	13.4	6.4	0.2	Winter '77° crushed	2.5
Birch-spruce uncrushed	13.4	8.2	3.5	Summer '77° crushed	2.7
Mature crushed	17.0	4.9	2.9	Winter '78° crushed	2.3
Mature uncrushed	20.9	11.0	3.1	Uncrushed° 'B'	2.3

* All of the traps used in 1977 were unmodified.
** All of the traps used in 1978 were modified.
° All Mystery Creek sites were black spruce.

APPENDIX B

Birds

In two summers of trapping, 98 birds were caught in traps set for small mammals. The crushed sites accounted for 55% of the total captures. Various kinds of sparrows were caught in the crushed sites. Gray jays (Perisoreus canadensis) and slate colored juncos (Junco hyemalis) comprised most of the captures in uncrushed sites. Most of the birds captured were caught at the Willow Lake area (90%). Birds seemed to follow the same general pattern of abundance in relation to site as did small mammals in 1977 (Appendix B. Table 1).

Birds are able to adapt to habitat disturbance more readily than mammals because of their greater mobility (Bock and Lynch 1970). While checking traps in the mature crushed site at Willow Lake and the Moose Research Center, woodpeckers were observed searching for insects among the downed trees. It is apparently common for birds to take advantage of a temporary food supply in such a manner (Bock and Lynch 1970).

The black spruce crushed site at Willow Lake was an excellent example of birds' ability to quickly find and move into an area once it becomes suitable. Various species of sparrows were abundant there during the July 1978 trapping period, but voles were scarce. This site was settled by voles a month later, indicating that birds can utilize disturbed sites much more readily than small mammals.

APPENDIX B. TABLE 1. The number of birds captured in each site per 1000 trap nights.

Site	Area and Date Sampled: Willow Lake 1977	Willow Lake 1978	Moose Research Ctr. 1978	Site	Mystery Creek 1978
Black spruce crushed	1.04	20.83	0	Summer '63* crushed	0
Black spruce uncrushed	6.25	6.94	0	Uncrushed* 'A'	4.17
Birch-spruce crushed	5.20	4.17	4.17	Winter '77* crushed	0
Birch-spruce uncrushed	6.25	4.17	0	Summer '77* crushed	2.08
Mature crushed	12.50	18.06	2.08	Winter '78* crushed	0
Mature uncrushed	13.54	6.94	2.08	Uncrushed* 'B'	6.25

* All black spruce sites.

The primary effect of crushing on bird populations was to change the bird species using the area. Some species will decline with crushing and others will increase. For example, spruce grouse (Canachites canadensis) avoid burned areas and it is expected that they will avoid crushed areas (Ellison, 1975). Crushed sites supported populations of birds such as white crowned sparrows (Zonotrichia leucophrys) that were associated with early successional stages. Crushing tended to increase the diversity and abundance of birds found in the study areas. A study specifically on birds would have to be conducted to show exactly to what extent crushing affects bird populations.

APPENDIX C

Parasites

Five cases of stomach parasites were found in red-backed voles caught in the Willow Lake area in 1977. All five of the infected animals came from the black spruce uncrushed site. The nematode parasite, Mastophorus mirius, is reported to be circumpolar in distribution but locally restricted to spruce forest types (Rausch 1952). Nematodes were not found in mammals caught in the Willow Lake area during 1978. They were present in red-backed voles caught at the Moose Research Center and Mystery Creek areas. In the Moose Research Center area, nematodes were found in two voles from the mature uncrushed site and in one vole from the mature crushed site. These two sites are adjacent to each other and infected voles were captured within a restricted location near their boundaries. Seven infected voles were caught in the Mystery Creek area, which is a black spruce type.

Several generalizations can be made about the parasites. All nematodes found in 1978 were located in the small lower chamber of the stomach. Most stomachs contained only a few of the parasites. The most nematodes found in one stomach was 12. The largest nematode recorded was 35 mm long. All nematodes found were taken from voles captured in fall trapping periods. Adults tended to be more susceptible to parasites than immatures.

Fleas appeared to be scarce on voles captured in 1977, but very abundant on all voles captured during the fall of 1978. It is not known what caused the increase in fleas from one year to the next. What effect this may have on the vole population is also unknown. (Three livers from voles caught in the Mystery Creek area had white spots on them. They were sent to Fairbanks for examination to determine if the spotting was disease or parasite caused.)

APPENDIX D

Predators

The immediate effect of crushing on predators was to provide greater opportunity to take prey. Crusher operators indicated that it is common for coyotes (Canis latrans) and raptors to follow the machines and take prey as it is flushed. This is a learned hunting method that undoubtedly benefits only a few individuals.

For most predators, the availability of prey species declines with crushing. Snowshoe hares (Lepus americanus) and red squirrels (Tamiasciurus hudsonicus) are absent in recently disturbed forest areas (Smith and Aldous 1947, Wolff and Zasada 1975, Hooven and Black 1976, Kirkland 1977). Vole populations increase only in mature crushed sites and even that increase may only be temporary. Crushing mature stands probably benefits weasels (Mustela erminea) since both protective cover and a large food supply is provided. This type of cover reduces hunting opportunity for larger carnivores and raptors.

APPENDIX E

Small Mammal Cycles

Perhaps the most exciting aspect of small mammal population ecology is the study of cycles. At very high densities, small mammals are known to virtually destroy all the vegetation in certain areas (Thompson 1955). Northern ecosystems tend to have higher occurrences of these outbreaks than more southerly regions. In almost all instances, these cycling vole populations occur in Microtus spp. rather than Clethrionomys spp. (Elton 1942). These high and low cycles are regularly spaced between peaks and much work has been done on their causes (Golley et al. 1975).

This study was not long enough to determine if small mammals on the Kenai Peninsula are cyclic, but data indicates that vole and shrew populations do fluctuate greatly. During limited work on the Kenai lowlands in 1970 (Ellison 1970), trap success ranged from 3.1 to 8.3 small mammals caught per 100 trap nights. Trapping success for this study was 8.9 small mammals caught per 100 trap nights. Extensive trapping on the Kenai Peninsula in 1974 (Fuller et al. 1974) indicated that small mammal populations were at very low densities compared to this study. Trapping success during 1974 averaged 0.9 small mammals caught per 100 trap nights. This tenfold difference is even more pronounced when the methods used are considered. The traps and baits used were similar in each, but investigators in 1974 set traps 25 feet

apart and in locations where they thought mammals were most likely to be captured. The highest success for any lowland sites studied in 1974 was one capture per 100 trap nights, with most lowland sites averaging 0.5 to 0.1 captures per 100 trap nights. Trapping success for this study ranged between 6.6 to 10.3 captures per 100 trap nights. Red-backed voles and masked shrews were the most common species captured in each of these studies. Other small mammal species were present, but at very low densities. In the 1974 study, pygmy shrews seemed to be completely absent as there were no captures in 30,000 trap nights.

Small mammal populations were reportedly high in 1973 (Fuller et al. 1974) as were snowshoe hare populations. In 1974, there was a crash in the snowshoe hare population on the Kenai Peninsula. Whether or not there was a connection between that and the corresponding decline in small mammal numbers is unknown. During this study, hares were still at low densities while small mammal populations were at relatively high densities.

Both red-backed voles and masked shrews can have very high populations in one year and very low populations in the next. The peaks are usually not at regular intervals and there are some questions as to whether this is true cycling or just a density response dependent on food supply. The theory has been put forth that red-backed voles and other generalists do not cycle in the true sense of the word, but only

respond to favorable conditions (Whitney 1976). In various studies red-backed voles cycled at different intervals and some populations failed to show any cycling behavior (Grant 1976).